

Molecular basis of plant stress

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Due to their sessile lifestyle, plants are exposed to a variety of stresses and have to develop ingenious mechanisms to avoid or cope with the consequences of extreme stress factors. Plant genomes have therefore evolved to meet environmental challenges and many plant genes are dedicated to stress protective mechanisms.

Examples of adverse environmental factors include drought, salinity, solar radiation (excess light or high light intensities, UV-light), extreme temperatures (heat and low temperature/freezing stress), and pollutants (heavy metals, herbicides). In addition, low concentrations of essential macro- and micronutrients or conditions that result in poor uptake of these nutrients are also perceived as stress by plants. For example, phosphate deficiency is one of the most common reasons for poor plant growth and reduced crop yield [1]. Sometimes, two and even more abiotic and/or biotic stress factors impose their effects simultaneously, so that plants have to deal with a multitude of challenges [2]. Oxidative stress is a common consequence of many of these factors.

To address the various adverse conditions, plants respond with diverse morphological and physiological adaptive mechanisms. Succulent plants, for example,

counteract drought by retaining water, while resurrection plants have developed ways to withstand the reduced water content and can even fall into anabiosis. Other examples are morphological changes of leaves such as leaf rolling or thickening wax layers, which are often observed in response to stresses such as drought, high light salt, temperature, heavy metals, UV radiation, or biotic challenges [3, 4]. Modifications in root architecture occur in response to many unfavorable abiotic factors, particularly osmotic and nutrient stresses [1, 5, 6]. The morphological and physiological changes are determined by molecular responses that govern global transcriptome, proteome, and metabolome adjustments, eventually resulting in stress protection, altered growth and development, or death in the worst scenario.

Identification of stress-related genes by mutant analysis and classic genetic approaches in combination with the recent advances in transcriptomics, proteomics, and metabolomics has uncovered a significant part of the vast and elaborate stress signaling network. This volume summarizes our understanding of the molecular events that lead from stress perception and signal transduction to various stress responses. The contributions in this multi-author review focus on different aspects of abiotic stress signaling, such as drought, osmotic stress, heavy metal stress, and phosphate deficiency, as well as general aspects of biotic and abiotic stress signaling related to protein phosphorylation, sumoylation, and metabolomic alterations during stress and development.

Several of the most frequently occurring abiotic stresses in nature, such as drought, salinity, and low temperature, cause osmotic stress. The first review of Hiroaki Fujii from the University of Turku, Finland, and Jian-Kang Zhu from Purdue University, USA, is dedicated on the SNF1-related protein kinases (SnRK2) kinases, which have key roles in

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osmotic stress responses and abscisic acid (ABA) signaling. These kinases, activated by osmotic stress and/or by ABA, act on various downstream targets to ensure rapid physiological responses and transcriptional regulation ultimately leading to stress protection. Overexpression of SnRK2s enhances growth even in the absence of stress, while mutation in SnRK2 can result in hypersensitivity to osmotic stress. The review presents the latest knowledge on SnRK2 regulation (regulation by phosphorylation, de-phosphorylation, Ca²⁺-regulation via an SnRK2-interacting calcium sensor) and SnRK2 targets. In addition, the authors present a brief overview of the other kinases involved in osmotic stress signaling.

The contribution of Ana Victoria Garcia, Mohamed Al-Yousif, and Heribert Hirt from the Plant Genomics Research Unit, France, focuses on the AGC kinases, another group of protein kinases that regulate various aspects of growth, metabolism, abiotic stress responses, and plant–microbe interactions. Some of these kinases phosphorylate key player proteins from the auxin- or blue light-signaling pathways, whereas others like PDK1 (3-phosphoinositide dependent kinase 1) integrate lipid-derived signals to modulate environmental stresses. Special attention is given to biotic stress and the modulation of programmed cell death. The interaction of AGCs with MAPK cascades during plant immunity is described in detail. The review also summarizes recent data on the role of AGC kinases in the relationship with growth-promoting endophytic fungi.

The article of Tsanko Gechev, Dorothea Bartels, and co-workers from the University of Plovdiv, Bulgaria, and the University of Bonn, Germany, describes the unique group of desiccation-tolerant plants. These plants, able to survive severe desiccation to air-dried state, are fundamentally different not only from drought-sensitive plants but also from other drought-surviving plants such as succulents or ephemerals. The review outlines known physiological and biochemical mechanisms contributing to the resurrection phenotype, and highlights the recent transcriptome, proteome, and metabolome data from several resurrection species subjected to desiccation and subsequent rehydration. The authors identify molecular responses that are common for both drought stress and desiccation, as well as molecular strategies that appear to be specific for desiccation-tolerant resurrection species. Authors conclude that some resurrection plants are already primed for desiccation, expressing genes and already accumulating protective metabolites under non-stress conditions; other specific features include high activation of existing protective mechanisms (LEA proteins, ELIPs, HSPs, accumulation of various sugars and powerful phenolic antioxidants) and activation of genes and metabolites unique to resurrection plants, such as *CDT-1*, *CpEti-9*, and 3, 4, 5 tri-*O*-galloylquinic acid.

An overview of the molecular mechanisms of heavy metal tolerance is presented by Mark Aarts and Ya-Fen Lin from Wageningen University, The Netherlands, with the focus on nutritional and non-nutritional metal homeostasis. Plants can be grouped into several categories according to the way they respond to heavy metal stress: sensitive species, resistant excluders, tolerant non-hyperaccumulators, and hypertolerant hyperaccumulators. Different strategies for coping with heavy metals are presented: reducing heavy metal bioavailability by bacteria or mycorrhizal fungi, preventing metals from entering root cells; reducing the metal influx by downregulation of transporters or enhanced metal efflux; chelation with nicotianamine, glutathione, phytochelatin, and metallothioneins, and/or sequestration in vacuoles (or/and in non-essential tissues/cells and old leaves). Increased concentrations of several heavy metals can lead to elevation of reactive oxygen species (ROS) levels. Detoxification of ROS and controlling ROS signaling pathways are other strategies to counteract heavy metal toxicity. The final part of this contribution presents an overview of the signal transduction network integrating heavy metal stress and ROS.

Deprivation from essential nutrients is also a life-threatening stress which negatively impacts plant health and productivity. The review of Kashchandra G. Raghothama and co-workers from Purdue University focuses on stress caused by low phosphate availability. The main topics are transcription factors involved in phosphate homeostasis, but other molecular mechanisms are also discussed. Various constitutively expressed and low phosphate-inducible transcription factors are reviewed. In depth analyses of the biological effects of mutating or overexpressing particular transcription factors are provided. In addition to the current knowledge on transcription factors regulated by phosphate starvation, the paper describes the cross-talk of transcription factors with plant hormones and sugar signals. Furthermore, various developmental effects linked to phosphate status, especially related to root development, are highlighted in the review.

Reversible post-translational modification of proteins by sumoylation appear to be as common as phosphorylation and play major roles during plant development, and biotic- and abiotic stress responses. Pedro Humberto Castro, Rui M. Tavares, Eduardo R. Bejarano, and Herl ander Azevedo from the Universities of Minho, Portugal, and M alaga, Spain, review the increasing literature on plant SUMO. The authors outline the sumoylation pathway, including the E1–E2–E3 cascade and various SUMO proteases, and compile the fast-growing number of SUMO targets that act as molecular links to hormonal, abiotic, and oxidative stress responses. Most of these SUMO targets are involved in regulation of gene expression and abiotic stress responses, and particular emphasis in the review is paid on

extreme temperatures, drought, salinity, and nutrient imbalance (phosphate starvation, copper and nitrogen homeostasis).

Many of the unfavorable abiotic factors and biotic challenges result in oxidative stress. There are several excellent reviews on ROS homeostasis and the role of ROS as modulators of plant stress responses [7–9]. The review of Bernd Mueller-Roeber and co-workers from the University of Potsdam, Germany, looks at ROS from another angle, highlighting the role of reactive oxygen species in plant growth. Growth and stress responses are intricately connected and the authors dissect the molecular mechanisms in these responses. After discussing evolutionary aspects of ROS signaling, the authors emphasise the role of ROS in cell proliferation and differentiation and the pleiotropic role of several ROS-related protein families (thioredoxins, glutaredoxins, peroxiredoxins, glutathione peroxidases, NADPH oxidases) in plant growth and development.

The recent development in metabolomics allows us to employ this technology to solve complex systems biology questions related to plant stress and development. Plant metabolism is dramatically altered during all types of stress. The metabolic network has to be re-programmed in order to assure plant survival, which is often accomplished by maintaining essential metabolism and synthesis of metabolites with stress-protective and signaling properties. Toshihiro Obata and Alisdair Fernie from the Max-Planck Institute of Molecular Plant Physiology, Potsdam-Golm, Germany, review the advances in metabolomics and give examples of plant metabolic networks under different types of abiotic stresses. The authors describe the most important and widely used techniques in metabolomics research, such as gas chromatography- and liquid chromatography-mass spectrometry, capillary electrophoresis, and nuclear magnetic resonance spectroscopy. Next, a comprehensive

overview of metabolic responses during a variety of stresses is given: drought, temperature stress, light stress (high light and UV radiation), salinity, heavy metals, nutrient starvation (carbon, nitrogen, phosphorus, and sulfur), and oxidative stress. Finally, the authors give examples of successful integration of metabolomics data with transcriptomics and proteomics to decipher the molecular mechanisms of plant stress responses.

We would like to thank all the colleagues for their valuable contributions, creating together a comprehensive picture of molecular responses towards abiotic and biotic stress responses.

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